

Home range shifts accompanying breeding in the Eastern Chipmunk, *Tamias striatus* (Rodentia: Sciuridae)

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Abstract

Capture-recapture techniques were used to study home ranges of 34 breeding and non-breeding male and female *Tamias striatus* over a nine week period. Results showed that reproductive males were of larger body size and had larger home ranges than non-reproductive males. Females attaining oestrus were also larger than non-reproductive females at the beginning but not at the end of the study. Also, females in oestrus had smaller home ranges than non-oestrus females and, for females that attained oestrus, breeding home ranges were smaller than pre- or post-oestrus home ranges. These results suggest that the breeding behavior of *Tamias* may involve home range adjustments made by both males and females.

Introduction

Mating behavior, availability of food and water resources, and local population density have all been implicated as factors affecting home range size in the eastern chipmunk, *Tamias striatus* (Linnaeus, 1758) (YERGER 1953; DUNFORD 1970; FORSYTH and SMITH 1973; TRYON and SYNDER 1973; MARES et al. 1976; YAHNER 1978; GETTY 1981a; BOWERS et al. 1990). For *Tamias*, permanently located burrows provide a fixed center of activity around which areas usually less than 1 ha (more typically, between 0.08 and 0.60 ha) are utilized on a periodic basis (BLAIR 1942; ICKES 1974; ELLIOTT 1978). Although substantial overlap in home ranges is common, central core areas are defended against conspecific neighbors (WOLFE 1966; DUNFORD 1970; ICKES 1974; YAHNER 1978; ELLIOTT 1978; GETTY 1981b). During the summer breeding period, males usually have home ranges that overlap with and may totally subsume the smaller ranges of females and non-breeding males (FORSYTH and SMITH 1973). Like many solitary, ground dwelling sciurids, *Tamias* has a polygynous mating system (EMLEN and ORING 1977), and the expansion of home ranges by breeding males is a way in which multiple females can be mated (YAHNER 1978; DOBSON 1984). Breeding females are thought to have home ranges that are not different from that of non-breeding females (e.g., ELLIOTT 1978).

In our studies of *T. striatus* in Virginia, USA, we have documented shifts in home ranges that involve both breeding males and females. Here we describe these shifts. Included are examinations of home range size of breeding and non-breeding individuals, and changes in home ranges of individual females that occur with the onset of oestrus.

Material and methods

Our study was conducted at the Blandy Experimental Farm, a biological field station of the University of Virginia located in the northern Shenandoah Valley at an elevation of 190 m in Clarke County, Virginia, USA (ca. 78°00W, 39°00N). Located in the central portion of the Farm is the 50–60 ha Orland E. White Arboretum that includes over 7,000 mostly large, mature native and exotic trees. Specimen plantings are separated by open fields, and running throughout are more than 2 km of loose

stone walls that were constructed over 100 years ago from rocks and boulders of dolomite origin. The understory of the Arboretum is mowed regularly. The open, parklike vegetation with a combination of thick canopy, open understory, and stone walls with numerous crevices affording refugia and burrowsites, creates favorable habitat for the eastern chipmunk (for further description of the site see BOWERS et al. 1990).

The population of chipmunks residing in the Arboretum was studied by capture/recapture techniques for 9 weeks from 1 June to mid-August, 1988. One-hundred eleven folding, Sherman live traps were placed within 1 m of stone walls at 15 m intervals. Traps were set 3–4 successive days during each of the 9 weeks, using cracked corn as bait, and were checked at dawn and dusk. To lessen mortality due to heat stress, traps were placed in cardboard shelters and closed during afternoons on particularly hot days ($> 30^{\circ}\text{C}$). Captured animals were weighed, sexed, fitted with a numbered eartag, and released. Sexual condition of all captured animals was recorded: males as scrotal or non-scrotal; females with swollen or non-swollen vulvas (see SMITH and SMITH 1975).

We use two measures of home range size: 1. the average distance between capture locations; and 2. the maximum distance between all capture locations. Use of linear estimates of home range size was justified because chipmunks showed strong affinities for the stone walls (i.e., in previous investigations they were rarely captured at traps > 5 m from the walls), producing home ranges that extended along walls and were largely one-dimensional (see BOWERS et al. 1990).

Results

Over the 9-week study period more than 3,400 trap nights produced over 400 captures of 58 chipmunks. We restrict our analyses here to only those 34 individuals (10 males and 24 females) captured four or more times. These individuals were captured an average of 10.7 ± 7.4 times each over the summer. During the study period four of the 10 males, and nine of 24 females attained breeding condition. Females were observed to be in oestrus between 5–14 July. Scrotal males weighed more than non-scrotal males, and animals of both sexes in breeding condition were captured significantly more often than reproductively inactive individuals (Tab. 1). Females that attained oestrus in July weighed less in

Table 1. Mean (\pm SD) body weights (in August), number of captures, and the average and maximum distance between trap captures (calculated over the nine-week study period) for breeding and non-breeding male and female *Tamias striatus*

Estimate	Females		Males	
	Breeding (n = 9)	Non-breeding (n = 15)	Breeding (n = 4)	Non-breeding (n = 6)
Body weight (g)	86.1 \pm 7.3	86.0 \pm 12.1	90.5 \pm 6.6	77.2 \pm 5.8
Number of captures	12.3 \pm 6.5	8.0 \pm 6.9	8.5 \pm 5.5	7.2 \pm 5.4
Mean distance (m)	35.5 \pm 21.0	43.7 \pm 36.8	77.4 \pm 40.1	25.3 \pm 23.8
Maximum distance (m)	93.2 \pm 54.6	88.2 \pm 72.0	160.3 \pm 40.2	51.8 \pm 43.9

June than did females not entering oestrus (61.4 ± 18.1 g versus 79.3 ± 20.2 g); by August there were no significant differences in body weights for females in these two groups (Tab. 1).

A two-way ANOVA testing for differences in home range size for the entire nine-week study period indicated no significant ($p > 0.10$) sex or breeding condition effect, but a significant sex by reproductive condition interaction (Tab. 2). This interaction is due to males in breeding condition having larger, and females who attained oestrus having smaller home ranges over the summer than sexually inactive individuals (Fig. 1).

These different responses by males and females could reflect behavioral changes associated with contrasting mating behaviors, or alternatively, they could reflect individual differences involving non-breeding factors (quality of home range, etc.; see BOWERS and SMITH 1979). A more rigorous test would examine changes in home range size for

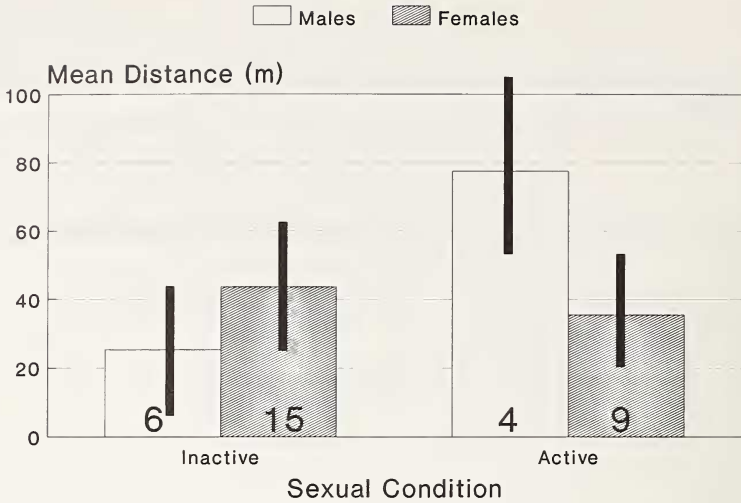


Fig. 1. Mean distance between capture locations (in meters) for breeding and non-breeding males and females. Standard errors of the mean are shown. The number of animals over which averages were calculated are given in each bar

Table 2. Summary of two-way ANOVA testing for sex by breeding condition differences in the two estimates of home range size

Source of variation	SS	DF	MS	F	P
Mean distance (m)					
Sex	196.7	1	196.7	0.20	0.66
Breeding condition	772.6	1	772.6	0.77	0.39
Sex by condition	6118.9	1	6118.9	6.06	0.02
Residual	30282.4	30	1009.4		
Total	37389.5	33	1133.0		
Maximum distance (m)					
Sex	126.2	1	126.2	0.03	0.86
Breeding condition	10358.8	1	10358.8	2.80	0.10
Sex by condition	18026.1	1	18026.1	4.85	0.03
Residual	110938.1	30	3697.9		
Total	139508.7	33	4227.5		

particular individuals over breeding and non-breeding periods. Such a test is possible for females who come in and out of oestrus over time periods of between three and nine days (SMITH and SMITH 1975), and is not possible for males who remain scrotal or non-scrotal for most of the summer months. In our study, nine females bred during the first two weeks of July, while 15 females failed to breed. Comparing home range estimates for individual females captured at least three times during pre-breeding, breeding, and post-breeding periods showed that females attaining oestrus had smaller home ranges during breeding relative to the home ranges of non-breeding females (Fig. 2, a test of difference between breeding and non-breeding chipmunks over the three periods using a repeated measures ANOVA; $F_{2,3} = 17.2$, $P = 0.023$ for mean capture distance; $F_{2,3} = 8.8$, $P = 0.055$ for maximum distance between captures).

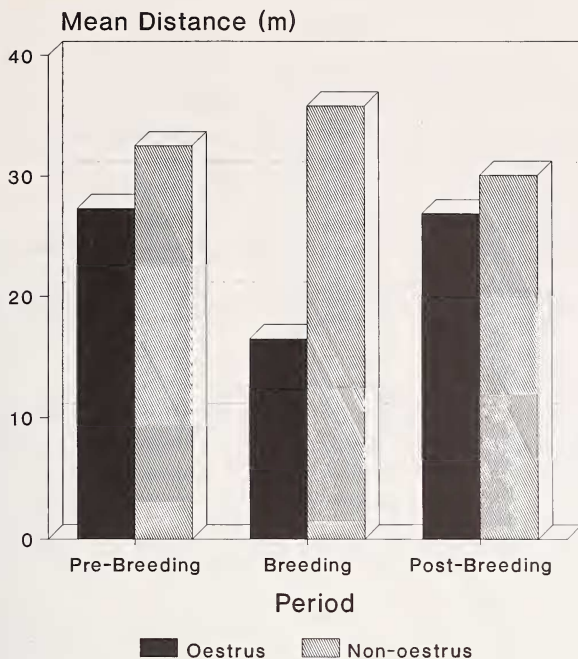


Fig. 2. Mean distance between capture sites (m) for females attaining oestrus (bars with dark shading) versus those that did not (light shading), and broken into three time-periods: i.e., pre-breeding (before 5 July), breeding (5–14 July), and post-breeding (after 14 July) periods. Females entering oestrus had significantly smaller home ranges relative to: 1. non-oestrus females during the breeding period; and 2. home ranges during pre- and post-breeding periods

Discussion

These results add to what is known about polygynous mating systems in solitary sciurids. *Tamias* has two mating periods (i.e. February–April, and early-to-mid July), both which may involve a variable proportion of the resident females (PIDDUCK and FALLS 1973; SMITH and SMITH 1972; ELLIOTT 1978). In our study females attaining oestrus in July were significantly smaller in June than females not breeding in July. This suggests that summer reproduction was performed by females born in the spring, and that larger females, as a group, may have bred in the spring but not the summer. By August there were no significant size differences between summer breeding and non-breeding females suggesting significant weight gains made by the summer breeders.

Our results also suggest that the reduction in home range size of females accompanying the onset of breeding, while more subtle, may be as indicative of the mating system of *Tamias* as home range expansion by breeding males. It is generally assumed that males expand their home ranges during breeding periods so as to achieve multiple matings (DOBSON 1984). During such periods breeding males converge towards home ranges of females in oestrus. This is accomplished through the use of olfactory cues that advertise the onset of oestrus (DOBROUKA 1972; KEEVIN et al. 1981). Successful mating is assured by female tolerance of males in core areas that are usually defended rigorously (YAHNER 1978). Limiting movements to certain portions of the home range would further increase the likelihood that breeding males could locate and copulate with resident females. Under

this scenario, reductions in size of home ranges may be a feature of the mating repertoire of female *Tamias* that leads to an increase in competition among males for mates, creating an arena where only the most fit males would breed.

This assumes that the dominant males, in fact, perform the majority of the breedings. However, for the eastern chipmunk a single female may copulate 10–30 times, and with many of the males available (ELLIOTT 1978). Similar breeding systems have been reported for the tassel-eared (FARENTINOS 1972) and gray squirrels (HORWICH 1972). In the former, a majority of the early matings were performed by the dominant males but in the latter there did not appear to be any relationship between dominance and breeding success. If, as FARENTINOS (1972) argues, the first copulations are most likely to result in fertilization, then reduction in breeding home ranges of females—and the concomitant aggregation of males—would assure that the most fit males do most of the matings irrespective of the total number of males that copulate.

As an alternative, home range reduction by breeding females may result from the harassment by males attempting to copulate. Some authors have noted that up to 12 males may accompany and actively pursue females in oestrus both before and after copulation (YAHNER 1978; ELLIOTT 1978). During such mating bouts females may seek refuge from suitors under ground, or in structurally complex microhabitats. Therefore, it may be that reductions in the home ranges of oestrus females result from the aggressiveness of males attempting to mate, and/or is a means by which females in oestrus avoid large male aggregates.

The exact cause of the reduction in breeding female home ranges would be important to the breeding system of the species because in one case females make themselves more available, and in the other, less available to breeding males. Specifically, female adjustments in home range size could either increase the degree to which *Tamias* is polygynous or place severe limits on it. That *Tamias* have highly synchronized oestrus periods could be viewed as evidence supporting the male-avoidance scenario because each female makes herself less available to local males than if oestrus was asynchronous (EMLEN and ORING 1977). Further study of the behavior of oestrus females in the presence and absence of breeding males, and the mating success of dominant and subordinate males is needed to distinguish between these alternatives.

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Zusammenfassung

Verschiebungen des Aktionsraumes beim Östlichen Streifenhörnchen Tamias striatus (Rodentia: Sciuridae) während der Fortpflanzung

Die Aktionsräume von 34 reproduktiven und nichtreproduktiven Männchen und Weibchen von *Tamias striatus* wurden über einen Zeitraum von 9 Wochen anhand markierter Wiederfänge bestimmt. Reproduktive Männchen waren größer und hatten größere Aktionsräume als Männchen, die nicht an der Fortpflanzung teilnahmen. Zu Beginn, aber nicht am Ende des Untersuchungszeitraumes waren östrale Weibchen ebenfalls größer als anöstrale. Die Aktionsräume östraler Weibchen waren kleiner als die anöstraler Weibchen, und während des Östrus waren die Aktionsräume kleiner als davor und danach. Die Resultate lassen vermuten, daß Verschiebungen in der Aktionsraumgröße bei beiden Geschlechtern von *Tamias* zur Fortpflanzungsbiologie gehören.

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